

Predicted Genetic Gain and Inbreeding Depression with General Inbreeding Levels in Selection Candidates and Offspring

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ABSTRACT

Methods for predicting response to selection in noninbred populations for individuals and family-based selection methods have been very well developed. However, theory to predict improvement of inbred lines derived from a recombined population, as well the predicted change in inbreeding depression rate, has not been developed. Prediction equations for general levels of inbreeding in both selection candidates and recombined offspring of selected parents for intrapopulation selection methods were developed. All common methods of individual, half-sib, and self-progeny selection were predicted to change inbreeding depression rates in a population if the covariance parameters D_1 and D_2^* were nonzero. However, the change in inbreeding depression rate was unaffected by additive genetic variance. It was further established that outbred selection in some maize (*Zea mays* L.) populations may be expected to increase inbreeding depression based on published estimates of the covariance parameter D_1 .

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THEORY FOR PREDICTING selection response in plant improvement programs has been very well developed for noninbred progeny (Empig et al., 1981; Cockerham and Matzinger, 1985; Nyquist, 1991; Holland et al., 2003). Selection response has nearly always been defined as the change in mean value of noninbred individuals in the population resulting from selection among various types of candidates or candidate families, including full-sib families, half-sib families, and/or progeny developed by self-pollination. Cockerham and Matzinger (1985) went one step further and predicted improvement in inbred lines developed directly from selected self-pollinated progeny lines. However, methods for predicting response to selection in plants have not been developed for inbred offspring derived from an improved population; that is, what impact will a particular selection method have on the performance of inbred lines derived from an improved population or on the rate of inbreeding depression in an improved population? If response to selection could be predicted for noninbred individuals ($F = 0$) and inbred individuals ($F = 1$) in an improved population, a prediction for the change in inbreeding depression would be readily obtainable as the difference in response rates between noninbred individuals and inbred individuals in the improved population. Such theory is needed for species in which hybrid cultivars are important, such as maize (*Zea mays* L.). The objective of this paper was to develop theory to predict the change in mean value of noninbred individuals and inbred individuals in a recombined population for individual, half-sib, and self-progeny

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selection and to use this theory to predict the expected change in inbreeding depression rate resulting from one cycle of selection.

MATERIALS AND METHODS

Pedigree

A generalized pedigree for formation of candidate families and passing of gametes to recombined individuals is shown in Fig. 1. Selection-candidate families were composed of half-sib or self-pollinated descendants of a single founder individual. Founder individuals were designated as P_m for male and P_f for female gametes that unite to form recombined individuals (R in Fig. 1) following selection. Predicted gains were developed to include formation of candidate families with any number of generations of descent from the founder individual, P_m or P_f , including zero generations if an individual was evaluated directly as a candidate for selection (mass selection). Development of candidate families could include a combination of self- and open pollination. For example, the founder of a family could be self-pollinated to obtain an S_1 line, and the S_1 line could then be planted ear-to-row and pollinated by the base population to form a half-sib family. Individuals in the recombined population, represented by individual R, were the result of a union of a male gamete, descended from individual P_m , and a female gamete, descended from individual P_f . Gametes uniting to form the zygote of individual R could have been directly obtained from individuals P_m and P_f , or they could have been generated by descendants of P_m and P_f that is, from remnant seed of the candidate family. All generations between individuals P_m or P_f and R were assumed to be either generations of self-pollination or open pollination. If the line of descent includes open pollination, it was assumed that one gamete descended directly through the line of descent between P_m or P_f and R and one gamete was sampled randomly from the reference population in each generation. Individual R was used as the basis to predict response in noninbred individuals. Individual R was subsequently self-pollinated to produce self-pollinated descendants, D, which were used as the basis to predict response in inbred individuals.

Genetic Model

The assumed model for this investigation was a single locus model (Fisher, 1918; Harris, 1964):

$$g_{ij} = \mu + \alpha_i + \alpha_j + \delta_{ij}$$

where g_{ij} = genotypic value of individual with genotype A_iA_j , μ = population mean, α_i = additive effect of i th allele, and δ_{ij} = dominance deviation.

From a single-locus genetic model, Harris (1964) extended genotypic covariances to any level of inbreeding. In the derivation of covariances, Harris (1964) defined additive effects of alleles, α_i and α_j , strictly with respect to a non-inbred reference population, meaning that solutions for the additive effects were obtained from Hardy-Weinberg genotypic frequencies. In contrast, Fisher (1941) defined additive effects given the actual genotypic frequencies in the population, which depend on the inbreeding level. Because of the way Harris (1964) defined additive effects, the expected values of additive effects at all inbreeding levels and dominance effects in noninbred individuals are

zero, that is, $E[\alpha_i] = 0$ and $E[\delta_{ij}] = 0$. However, among a sample of inbred individuals, the expectation of dominance deviations is equivalent to a weighted sum of homozygous dominance deviations, $E[\delta_{ii}] = \sum_i p_i \delta_{ii} = h$ (where p_i = frequency of i th allele), which is nonzero. Cockerham (Cockerham, 1983; Wright and Cockerham, 1986) defined the expectation of homozygous dominance deviations as inbreeding depression. From the expectations of noninbred and inbred individuals, it can be seen that Cockerham's definition of inbreeding depression is equivalent to the mean of inbred individuals minus the mean of noninbred individuals:

$$E[\mu + \alpha_i + \alpha_j + \delta_{ij}] = \mu \text{ for noninbred individuals}$$

$$E[\mu + 2\alpha_i + \delta_{ii}] = \mu + \sum_i p_i \delta_{ii} = \mu + h \text{ for inbred individuals}$$

and

$$E[\mu + 2\alpha_i + \delta_{ii}] - E[\mu + \alpha_i + \alpha_j + \delta_{ij}] = h$$

Covariances between noninbred individuals require only the two covariance components, σ_A^2 and σ_D^2 , whereas up to five components are required for covariances between inbred individuals (Harris, 1964). The three additional components required for inbred relatives, D_1 , D_2^* , and H^* , are related directly to the homozygous dominance deviations, the basis for inbreeding depression (Table 1). The component D_2^* is the variance of the homozygous dominance deviations, which parallels the dominance variance, σ_D^2 , except that D_2^* is defined strictly

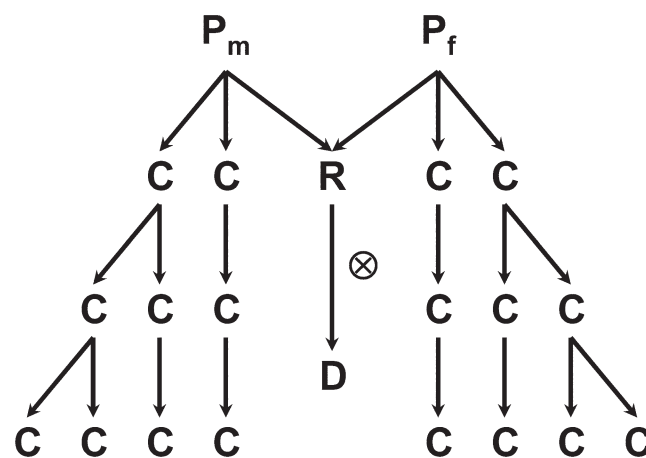


Figure 1. General representation of pedigree structure of male and female candidates and recombined individuals. Individuals P_m and P_f were male and female candidates or originating parents of candidate families. Individuals labeled C were individuals within candidate families that were evaluated phenotypically for selection (selection units). Individual R was a descendant of the original parents, P_m and P_f , of two selected families. Individual R was formed from the union of a female gamete, derived directly from individual P_f or from a descendant of P_f (i.e., from remnant seed) and a male gamete derived from individual P_m or from a descendant of P_m . Each arrow represents a line of descent that can include more than one generation and can represent the inheritance of two gametes, as in self-pollination, or a single gamete in the case of half-sib offspring of an individual. In the half-sib case, the gamete not shown in the figure was always assumed to be randomly sampled from the reference population. Individual D was a direct descendant of R obtained by self-pollination without selection.

Table 1. Genotypic covariance components for inbred relatives, their definitions, and coefficients in the general genotypic covariance between individuals X and Y.

Component	Expectation	Coefficient	Description
σ_A^2	$\Sigma_i p_i \alpha_i^2$	$2\theta_{XY}$	Additive variance
σ_D^2	$\Sigma_i p_i p_j \delta_{ij}^2$	$2(\Delta_{\ddot{X}+\ddot{Y}} - \delta_{\ddot{X}\ddot{Y}})$	Dominance variance
D_1	$\Sigma_i p_i \alpha_i \delta_{ii}$	$2(\gamma_{X\ddot{Y}} + \gamma_{\ddot{X}Y})$	Covariance between additive effects and homozygous dominance deviations
D_2^*	$\Sigma_i p_i \delta_{ii}^2 - (\Sigma_i p_i \delta_{ii}^2)^2$	$\delta_{\ddot{X}\ddot{Y}}$	Variance of homozygous dominance deviations
H^*	$(\Sigma_i p_i \delta_{ii}^2)^2$	$\Delta_{\ddot{X}\cdot\ddot{Y}} - F_X F_Y$	Sum of homozygous dominance deviations (inbreeding depression), squared

for dominance deviations in individuals with alleles identical by descent. Dominance deviations exist between alleles that are identical by descent because the additive effects are defined with respect to noninbred individuals and, hence, do not predict the genotypic value of an inbred individual in Harris's (1964) parameterization. The component H^* is equivalent to the sum (over loci) of homozygous dominance deviations, squared, and in general contributes little to the covariances between related individuals (Cockerham, 1983). The term D_1 is the covariance between additive effects and homozygous dominance deviations and is unique among genotypic covariance components in that it can be positive or negative. Interpretation of the component D_1 is difficult, but perhaps the most important implication of the component is its contribution to the covariance between inbred and outbred performance (Edwards and Lamkey, 2002, 2003). Collecting all five components into a single expression for the covariance between individuals X and Y produced (Harris, 1964; Cockerham, 1983; Cockerham and Weir, 1984; Wright and Cockerham, 1986)

$$\text{Cov}(X, Y) = 2\theta_{XY}\sigma_A^2 + (\Delta_{\ddot{X}+\ddot{Y}} - \delta_{\ddot{X}\ddot{Y}})\sigma_D^2 + 2(\gamma_{X\ddot{Y}} + \gamma_{\ddot{X}Y})D_1 + \delta_{\ddot{X}\ddot{Y}}D_2^* + (\Delta_{\ddot{X}\cdot\ddot{Y}} - F_X F_Y)H^* \quad [1]$$

where θ_{XY} , $\Delta_{\ddot{X}+\ddot{Y}}$, $\delta_{\ddot{X}\ddot{Y}}$, $\gamma_{X\ddot{Y}}$, $\gamma_{\ddot{X}Y}$, $\Delta_{\ddot{X}\cdot\ddot{Y}}$, F_X , and F_Y are identity-by-descent probabilities for two, three, or four alleles

Table 2. Identity-by-descent probabilities required for covariances between inbred relatives for two individuals. Individual X had alleles X_1 and X_2 and individual Y had alleles Y_1 and Y_2 . Each identity-by-descent probability is an average probability of identity of the allelic equivalencies shown in the second column. Notation for components was obtained from Cockerham (1971).

Measure	Equivalent sets of alleles
F_X	$X_1 \equiv X_2$
F_Y	$Y_1 \equiv Y_2$
θ_{XY}	$X_1 \equiv Y_1$ or $X_1 \equiv Y_2$ or $X_2 \equiv Y_1$ or $X_2 \equiv Y_2$
$\gamma_{X\ddot{Y}}$	$X_1 \equiv X_2 \equiv Y_1$ or $X_1 \equiv X_2 \equiv Y_2$
$\gamma_{X\ddot{Y}}$	$Y_1 \equiv Y_2 \equiv X_1$ or $Y_1 \equiv Y_2 \equiv X_2$
$\Delta_{\ddot{X}\cdot\ddot{Y}}$	$X_1 \equiv X_2, Y_1 \equiv Y_2$
$\Delta_{\ddot{X}+\ddot{Y}}$	$X_1 \equiv Y_1, X_2 \equiv Y_2$ or $X_1 \equiv Y_2, X_2 \equiv Y_1$
$\delta_{\ddot{X}\ddot{Y}}$	$X_1 \equiv X_2 \equiv Y_1 \equiv Y_2$

(Harris, 1964; Cockerham, 1971; Table 2). Identity-by-descent probabilities are nonmutually exclusive probabilities of combinations of two, three, or four alleles being identical by descent and were described in detail by Cockerham (1971) as functions of 15 mutually exclusive identity states. The probabilities θ_{XY} , F_X , and F_Y are the more commonly known coancestry coefficient between X and Y (θ_{XY}) and the inbreeding coefficients of X and Y (F_X and F_Y). Lange (2002) provided a highly accessible description for a set of 15 mutually exclusive identity states for sets of up to four alleles, which included a straightforward graphical representation, but

Lange's (2002) system did not include the eight nonmutually exclusive identity-by-descent probabilities needed for covariances of inbred relatives.

Genetic Gain Equation

A prediction equation was derived explicitly from the conditional normal distribution shown in the Appendix to maintain explicit accounting of candidate and offspring means, because population means may be affected by inbreeding depression. Genetic values were expressed as deviations from candidate and offspring population means, which account for inbreeding depression, in Appendix Eq. [A3]. Equation [A3] was reduced to genetic gain with the selection differential, S , representing the deviation of the mean of selected candidates from the mean of all candidates and ΔG representing the deviation of offspring of selected candidates from the expected mean of offspring derived from unselected candidates (Eq. [A4]):

$$\Delta G = pS \frac{\sigma_{C,O}}{\sigma_{G(C)}^2 + \sigma_{E(C)}^2} = pi \frac{\sigma_{C,O}}{\sigma_{P(C)}^2} \quad [2]$$

where $\sigma_{C,O}$ = covariance between candidates and offspring, $\sigma_{P(C)}^2$ = phenotypic variance of candidates, $\sigma_{G(C)}^2$ = genotypic variance of candidates, $\sigma_{E(C)}^2$ = environmental variance of candidates, p = parental control, S = selection differential, and i = standardized selection differential. The genetic portion of the predicted gain equation required two genotypic covariances, the covariance between candidates and offspring, $\sigma_{C,O}$, in the numerator and the genotypic variance of candidates in the denominator.

Covariance between Candidates and Offspring

The covariance in the numerator of genetic gain, $\sigma_{C,O}$, required the genotypic covariance between candidate individuals, C and recombined offspring individuals, D or R in the generalized pedigree in Fig. 1. The genotypic covariance between individuals C and D or R in turn required computation of up to eight identity-by-descent probabilities. Probabilities were computed by the expansion method of Cockerham (1971, 1983) in which probabilities are expanded through a pedigree from descendants, C, D, and R, to common ancestors P_m and P_f (Fig. 1). As described in the "Pedigree" section, above, expansions were developed to include any number of selfing and outcrossing generations between the progenitor of the candidate family, P, and candidate family members C or recombined offspring R (Fig. 1).

The coancestry coefficient, θ_{CD} , was expanded first because it appeared in the simplification of several other

expansions. Individuals C and D (Fig. 1) were both descendants of individual P, with individual P being the last common ancestor. Equation [A6] was used to obtain $\theta_{CD} = \theta_{CR} = \left(\frac{1}{2}\right)^{h_R+h_C} \theta_{PP}$ where h_R and h_C are the number of outcross generations between the common ancestor P and descendants R and C, respectively. The coancestry of an individual with itself was $\theta_{PP} = \frac{1}{2}(1 + F_P)$, which produced (Cockerham, 1983)

$$\theta_{CD} = \theta_{CR} = \left(\frac{1}{2}\right)^{h_R+h_C+1} (1 + F_P) = \theta_0 (1 + F_P) \quad [3]$$

where $\theta_0 = \left(\frac{1}{2}\right)^{h_R+h_C+1}$. The term θ_0 can be interpreted as the coancestry between C and D if individual P was not inbred.

The three-allele measure, γ_{CD} , was expanded next because it appeared in two subsequent expansions. If individual C was an outcross, $\gamma_{CD} = \gamma_{CR} = 0$. For candidates developed by self-pollination, γ_{CD} was first expanded from individual D to P, using Eq. [A5] and [A6] to obtain $\gamma_{CD} = \gamma_{CR} = \left(\frac{1}{2}\right)^{h_R} \gamma_{CP}$. The expansion of γ_{CP} from C to P, assuming C was derived from P by self-pollination with no outcross generations, was obtained from an expression given by Cockerham (1983), $\gamma_{gg'} = \frac{1}{2}(F_t + F_{g'})$. Individuals P and C were substituted into Cockerham's expression with generation $t = g'$ for individual P and generation g for individual C which resulted in $\gamma_{CP} = \frac{1}{2}(F_P + F_C)$. Substituting γ_{CP} into the expression for γ_{CD} and γ_{CR} resulted in:

$$\begin{aligned} \gamma_{CD} = \gamma_{CR} &= \left(\frac{1}{2}\right)^{h_R} \frac{1}{2}(F_P + F_C) \\ &= \left(\frac{1}{2}\right)^{h_R+h_C+1} (F_P + F_C) = \theta_0 (F_P + F_C) \end{aligned} \quad [4]$$

(using $h_C = 0$ because C was derived by self-pollination).

The remaining descent measures, γ_{CD} , $\Delta_{C,D}$, Δ_{C+D} , and δ_{CD} , which were functions of two alleles in individual D, were expanded by Eq. [A7] with individual D as the descendant, D, individual C as the constant individual X and individual R as individual A in Eq. [A7]:

$$\phi_{CD} = \frac{\phi_{CR}(F_D - F_R) + \phi_{CR}(1 - F_D)}{1 - F_R} \quad [5]$$

Because individual R was noninbred, $F_R = 0$ and $\phi_{CR} = 0$, which resulted in a simplified expansion from D to R: $\phi_{CD} = F_D \phi_{CR}$. The measure ϕ_{CD} represents any descent measure that was a function of a pair of alleles in D. Substituting specific descent measures for the generic measures, ϕ_{CD} and ϕ_{CR} , using the reduced form of Eq. [A7] and Table A1, resulted in the following expressions:

$$\begin{aligned} \Delta_{C,D} &= F_D F_C, \\ \gamma_{CD} &= F_D \theta_{CR} = \theta_0 F_D (1 + F_P), \\ \Delta_{C+D} &= \\ F_D \gamma_{CR} &= \begin{cases} 0 & \text{if C is outcrossed} \\ \theta_0 F_D (F_P + F_C) & \text{if C is self-pollinated} \end{cases} \end{aligned} \quad [6]$$

and

$$\begin{aligned} \delta_{CD} &= \\ F_D \gamma_{CR} &= \begin{cases} 0 & \text{if C is outcrossed} \\ \theta_0 F_D (F_P + F_C) & \text{if C is self-pollinated} \end{cases} \end{aligned} \quad [7]$$

Four allele descent measures for the relationship between C and D were substituted into the general covariance between two individuals (Cockerham and Weir, 1984; Cockerham, 1983; Wright and Cockerham, 1986) to obtain covariances between individuals C and D for three types of candidates: individuals (individual C is equivalent to P_m or P_f), half-sib families (C is an outcross), and families derived by self-pollination. Formulas for individuals as candidates were obtained directly from the case in which candidate families were developed by self-pollination with $F_C = F_P$. In the covariance between individuals C and D, the terms σ_D^2 and H^* canceled from the genotypic covariance between C and D because $\Delta_{C,D} = \delta_{CD}$ and $\Delta_{C,D} = F_D F_C$. Inbred individuals C and D were assumed to be derived by self-pollination, so substitution of values of F_D and F_C must be only those values attainable by self pollination, $F_C = 1 - (1/2)^g(1 - F_P)$ and $F_D = 1 - (1/2)^g$ (noting that $F_R = 0$). The inbreeding level of individual P, F_P , however, could take on any value.

Coefficients for individual components in the genotypic covariance between candidates and offspring, $\sigma_{C,O}$, are summarized in Table 3 for general inbreeding levels of individuals P, C, and D. The predicted change in inbreeding depression rate, that is, selection response for inbreeding depression, was predicted by subtracting the predicted change in noninbred individuals ($F = 0$) from predicted change in inbred individuals ($F = 1$).

Variance of Candidates

The genotypic variance, $\sigma_{G(C)}^2$, of candidates took slightly different forms for different types of candidates. For individuals, the variance reduced to a function of the candidate individuals inbreeding coefficient (Cockerham, 1983):

$$\begin{aligned} \sigma_{G(C)}^2 &= (1 + F_C)\sigma_A^2 + (1 - F_C)\sigma_D^2 \\ &\quad + 4F_C D_1 + F_C D_2^* + F_C (1 - F_C)H^* \end{aligned} \quad [8]$$

General expressions for genotypic variances of candidate family means are given in the Appendix for up to three generations of self-pollination and or outcrossing to produce adequate seed quantities for replicated evaluation experiments. As the number of individuals sampled within a family in the first generation increases, the genotypic variance of a family mean approaches the covariance between two individuals with the last common ancestor being the single founder-individual of the family (individual P_m or P_f in Fig. 1; Eq. [A8–A10]). The asymptotic genotypic variance for an outbred family derived from h generations of outcrossing from a single founder with inbreeding coefficient F_P is derived from Eq. [A8]:

$$\sigma_{G(C)}^2 = \left(\frac{1}{2}\right)^{2h} (1 + F_P)\sigma_A^2 \quad [9]$$

If the family was developed by a combination of self- and open pollination, the same formula can be used with h equal to the number of outcross generations. For example, if an individual is self-pollinated to produce an S_1 line, and the S_1 line is subsequently planted ear-to-row, emasculated, and allowed to open pollinate with the base population as a pollinator, there were two generations of increase, but only one generation of outcrossing, so $h = 1$.

Cockerham (1983) gave covariances between individuals derived exclusively from self-pollination. The asymptotic genotypic variance of a family mean with individuals with

Table 3. Coefficients required for computation of the covariance, $\sigma_{C,O}$, between candidates (C in Fig. 1) and offspring (D in Fig. 1) in the numerator of predicted genetic gain. Coefficients for outcrossed candidates, self-pollinated candidates, and individuals (P_m and P_f) with two levels of inbreeding of offspring (D in Fig. 1) were expressed as functions of inbreeding coefficients of individuals. The covariance, $\sigma_{C,O}$, between individuals C and D was obtained by multiplying coefficients in the Table for each variance component by $2\theta_0$. It was assumed that individuals C and D were developed by self-pollination, and hence their inbreeding coefficients must satisfy $F_C = 1 - (1/2)^g(1 - F_p)$ and $F_D = 1 - (1/2)^g$. The inbreeding coefficient F_p for individuals P_m and P_f could take any value from zero to 1.

Component†	Case	General	$F_D = 1$	$F_D = 0$	Difference
σ_A^2	All	$1 + F_p$	$1 + F_p$	$1 + F_p$	0
D_1	Outcross	$F_D(1 + F_p)$	$1 + F_p$	0	$1 + F_p$
	Self	$F_C + F_p + F_D(1 + F_p)$	$1 + F_C + 2F_p$	$F_C + F_p$	$1 + F_p$
	Individual	$2F_p + F_D(1 + F_p)$	$1 + 3F_p$	$2F_p$	$1 + F_p$
D_2^*	Outcross	0	0	0	0
	Self	$1/2 F_D(F_C + F_p)$	$1/2 (F_C + F_p)$	0	$1/2 (F_C + F_p)$
	Individual	$F_D F_p$	F_p	0	F_p

†Genotypic covariance components are defined in Table 1.

inbreeding coefficient F_C derived from a single founder with inbreeding coefficient F_p was (Cockerham, 1983) as follows:

$$\sigma_{G(C)}^2 = (1 + F_p)\sigma_A^2 + \frac{(1 - F_c)^2}{(1 - F_p)}\sigma_D^2 + 2(F_C + F_p)D_1 + \left[F_p + \frac{(F_C - F_p)^2}{2(1 - F_p)} \right] D_2^* + \frac{F_p(1 - F_C)^2}{(1 - F_p)} H^* \quad [10]$$

Common Selection Methods

Predicted response to selection was obtained for nine common recurrent selection programs summarized in Tables 4 and 5. For each method, the numerator of predicted response to selection was obtained by multiplying coefficients from Table 3 by the quantity $2p\theta_0$ from Table 5. Values for the number of outcross generations, h , and for number of parents on which selection was applied, p , were obtained by determining appropriate

numbers of self- and outcross generations in the general pedigree in Fig. 1. For mass selection, selection was applied directly to individuals P_m and P_f in Fig. 1, so there were no outcross generations. Recombination was accomplished by the random exchange of pollen among P_m or P_f and contemporaries. Response was measured in individual R. Selection was on a single parent (i.e., no selection on the male parent in Eq. [A3]) if parents were selected after pollination ($p = 1$ in Table 5). For half-sib methods, candidate families originated from a single open-pollinated individual. Alternatively, a single individual was self-pollinated to obtain an S_1 line, which was planted in isolation, emasculated, and harvested in bulk to obtain a larger seed quantity of seed (S_1 -topcross method). The minimum of outcross generations for half-sib methods was with the S_1 -topcross method with S_1 seed used for recombination. In this method, the only outcross in recombination of selected families occurred when S_1 individuals were mated with S_1 individuals from other selected, but unrelated, families. Tables 4 and 5 list several common recurrent selection methods based on half-sib and self-pollinated families. However, expressions in Table 3 can be applied to a much wider set of possible methods by using the same logic as that used to obtain parameter values in Table 5.

RESULTS AND DISCUSSION

Most previous treatments of predicted genetic gain have not done enough to address inbreeding in either candidates or recombined offspring of selected parents (Empig et al., 1981; Fehr, 1987; Nyquist, 1991; Holland et al., 2003). Wright and Cockerham (1986) provided a detailed analysis of selection among candidates derived by self-pollination, but genetic gain was limited to the direct descendents of the candidates arising from additional generations of self-pollination. The results presented here extend genetic gain to include any level of inbreeding among candidates of selection and any level of inbreeding among recombined offspring of selected candidates. Extension to multiple levels of inbreeding in recombined offspring leads to a direct method to estimate the impact of selection on inbreeding

Table 4. Descriptions of common recurrent selection programs.

Method†	Candidates	Recombined
Mass-BP	Individuals selected before pollination	Individual
Mass-AP	Individuals selected after pollination (selection only on female)	Individual
Half-sib-1	Half-sib progeny of one individual (1 generation of outcrossing)	Remnant half-sib seed
Half-sib-2	Half-sib progeny of one individual planted ear to row, topcrossed to population and harvested in bulk (2 generations of outcrossing)	Remnant half-sib seed from second generation (same generation as tested)
Half-sib-TT	S_1 -line (self-progeny of one individual) planted ear to row, topcrossed to population and harvested in bulk	Remnant topcross seed
Half-sib-TS	S_1 -line (self-progeny of one individual) planted ear to row, topcrossed to population and harvested in bulk	Remnant self-pollinated seed
Modified ear to row	Half-sib progeny of a single individual	Remnant half-sib seed (same season)
Self-progeny-1	Self-progeny of a single individual	Remnant self-pollinated seed
Self-progeny-2	Self-progeny of a single individual planted ear-to-row, self pollinated, and harvested in bulk (i.e., second generation self-progeny)	Remnant self-pollinated seed

†BP, before pollination; AP, after pollination; TT, topcrossed candidate, remnant topcross seed; TS, topcrossed candidate, remnant self-pollinated seed.

depression by comparison of response in noninbred offspring of selected candidates and inbred offspring derived from the improved population. Even with the extension to any inbreeding level, the genotypic covariances in the genetic gain equation summarized in Tables 3 and 6 reduced to three equations corresponding to three classes of selection candidates, individuals, half-sib families, and self-pollinated families. Furthermore, the three covariance expressions in the numerator and denominator of genetic gain reduced to functions of only two types of identity probabilities, the inbreeding coefficient and the coancestry coefficient, which are functions of only 2 alleles. In contrast, the completely general genotypic covariance between two individuals is a function of five distinct types of identity-by-descent probabilities (F , θ , γ , $\Delta_{\ddot{x}\ddot{y}}$, $\delta_{\ddot{x}\ddot{y}}$, $\Delta_{\ddot{x},\ddot{y}}$), which are functions of identity of up to four alleles. At the same time that this rather remarkable level of simplification was obtained, the final solution was quite broadly applicable to any selection method with a pedigree corresponding to the pedigree in Fig. 1 and meeting certain criteria: (i) P_m and P_f are unrelated, (ii) there are no pedigree loops in development of candidate families or individual R, and (iii) candidates and individual R are developed by some combination of self-pollination and random outcrossing (random sampling of gametes from the base population). Even within these seemingly restrictive conditions, the general pedigree in Fig. 1, including general inbreeding levels for P_m and P_f can be used to model a tremendous array of selection methods, including methods in Table 4 and any others within the imagination of the breeder.

Predicted response to selection was a function of intensity, environmental variance(s), experimental design, and pedigree structure of candidates and recombination units. Given the number of variables involved, it was difficult to make general comparisons among methods. Consider the simple example of half-sib selection versus S_1 -line selection assuming no dominance and equal environmental variances (environmental variance being the variance of errors on a family-mean basis):

$$\Delta G_{S_1} = i \frac{\sigma_A^2}{\sqrt{\sigma_A^2 + \sigma_E^2}} \quad [11a]$$

$$\Delta G_{HS} = i \frac{1/4 \sigma_A^2}{\sqrt{1/4 \sigma_A^2 + \sigma_E^2}} \quad [11b]$$

and

$$\frac{\Delta G_{S_1}}{\Delta G_{HS}} = 4 \sqrt{\frac{1/4 \sigma_A^2 + \sigma_E^2}{\sigma_A^2 + \sigma_E^2}} \quad [11c]$$

Table 5. Parameter values for obtaining the numerator, $2p\sigma_{C,O}$, of the predicted genetic gain equation for nine methods of recurrent selection described in Table 4. General pedigree showing candidate families, parents of candidate families, and recombined individuals is shown in Fig. 1.

Type	Method	Candidates [†]			Offspring [†]				θ_0^{\S}	$2p\theta_0$
		Family	g_C	h_C	Recombine	g_R	h_R	p		
Individual	Mass-AP	Individual	0	0	P	1	1	1	$1/4$	$1/2$
Individual	Mass-BP	Individual	0	0	P	1	1	2	$1/4$	1
Outcross	Half-sib-1	Half-sib	1	1	Half-sib	2	2	2	$1/16$	$1/4$
Outcross	Half-sib-2	Half-sib	2	2	Half-sib	3	3	2	$1/64$	$1/16$
Outcross	Half-sib-TT	S_1 -topcross	2	1	S_1 -topcross	3	2	2	$1/16$	$1/4$
Outcross	Half-sib-TS	S_1 -topcross	2	1	S_1	2	1	2	$1/8$	$1/2$
Outcross	Modified ear to row	Half-sib	1	1	Half-sib	2	2	1	$1/16$	$1/8$
Self	Self-progeny-1	$S_{g:g+1}$	1	0	$S_{g:g+1}$	1	1	2	$1/4$	1
Self	Self-progeny-2	$S_{g:g+2}$	2	0	$S_{g:g+2}$	2	1	2	$1/4$	1

[†] g_C = total number of generations of descent in candidate families from parent individual P_m (male) or P_f (female); h_C = number of outcross generations in development of candidate families.

[†] g_R = total number of generations from parent individual P_m or P_f and a recombined individual, R; h_R = number of outcross generations between individual P_m or P_f and recombined individual, R; p = parental control, i.e., number of selected parents of R.

[§] θ_0 = coancestry between candidate individuals, C, and recombined individuals R if parent P_m or P_f is noninbred.

Even under these simple conditions, the comparison between half-sib selection and S_1 selection did not reduce to a constant. The ratio of expected responses was bounded by 4 as σ_A^2 approaches zero and 2 as σ_E^2 approaches zero; that is, response of S_1 selection approaches four times the response of half-sib selection as heritability approaches zero and approaches two times the response of half-sib selection as heritability approaches one. If there was dominance, predicted response for S_1 -selection was

$$\Delta G_{S_1} = i \frac{\sigma_A^2 + 1/2 D_1}{\sqrt{\sigma_A^2 + 1/4 \sigma_D^2 + D_1 + 1/4 D_2^* + \sigma_E^2}} \quad [12]$$

If dominance was considered, there was no simple ratio to compare half-sib and S_1 selection, particularly considering that D_1 can be positive or negative. Such comparisons have occasionally led to optimistic predictions for inbred-progeny selection, but the predictions have not been validated by empirical research (Comstock, 1964; Wright and Cockerham, 1986; Coors, 1999). Although general comparisons among methods were difficult, the results shown in Table 3 reveal some noteworthy patterns.

The coefficient on additive genetic variance in the numerator of predicted gain, $2p\theta_0(1 + F_p)$, depended only on the inbreeding level of the founder individual, P, of candidate families and did not depend on subsequent inbreeding of candidate families, F_C , or offspring, F_D . Because the difference between predicted response in inbred offspring and predicted response in noninbred offspring was equal to the predicted change in inbreeding depression rate, additive genetic variance did not contribute to changes in inbreeding depression. This particular result provides some intuitive comfort in the underlying theory because it is not conceptually expected that additive variance (or additive effects)

Table 6. Coefficients for individual variance components in the denominator of selection response for three different classes of candidates of selection.

Candidate	σ^2_A	σ^2_D	D_1	D_2^*	H^*
Individual	$1 + F_p$	$1 - F_p$	$4F_p$	F_p	$F_p - F_p^2$
Half-sib	$(1/2)^{2h}(1 + F_p)$	0	0	0	0
Self	$1 + F_p$	$(1 - F_C)^2/(1 - F_p)$	$2(F_C + F_p)$	$F_p + (F_C - F_p)^2/2(1 - F_p)$	$F_p[(1 - F_C)^2/(1 - F_p)]$

should impact inbreeding depression. Whereas the coefficient on additive variance was always zero in the numerator of predicted change in inbreeding depression rate, the coefficient on D_1 was also identical for all methods with a value of $2p\theta_0(1 + F_p)D_1$. However, the impact of the component D_2^* , which did vary among methods, must also be considered in predicted changes in inbreeding depression. Two broad categories of candidates emerge from Table 3: noninbred candidates, which have only the component D_1 in predicted change in inbreeding depression; and inbred candidates, in which both D_1 and D_2^* appear in the numerator of predicted change in inbreeding depression rates.

The numerator of predicted change in inbreeding depression rate for selection among noninbred candidates, either individuals with $F_p = 0$ or half-sib families, was $2p\theta_0(1 + F_p)D_1$. The component D_1 is a covariance that can be positive or negative. As outlined in the “Materials and Methods” section, the expected value of noninbred individuals was equivalent to μ , and the expected value of inbred individuals was $\mu + \sum p_i \delta_{ii}$, so that the expectation of inbreeding depression was defined here and by Cockerham (1983) as $\sum p_i \delta_{ii}$. If inbred individuals have lower values than noninbred individuals, such as for grain yield of many crop species, the value of expected inbreeding depression, $\sum p_i \delta_{ii}$, is negative according to this definition. Unfortunately, only three sets of published estimates of D_1 in crop species, all in maize, are known to the author (Coors, 1988; Edwards and Lamkey, 2002; Wardyn et al., 2007). In all three sets of estimates, D_1 tended to be negative for most traits, or near zero in some cases. If D_1 is negative, a negative change in $\sum p_i \delta_{ii}$ is predicted. For grain yield in maize, for example, inbreeding depression is negative (inbred individuals have much lower yield than noninbred individuals), so a negative change in inbreeding depression results in a larger negative value; that is, selection among noninbred candidates increases the magnitude of inbreeding depression.

When candidates were inbred, including inbred individuals and lines derived by self-pollination, predicted change in inbreeding depression rate included both D_1 and D_2^* in the numerator of predicted gain. Because two components were involved, one of which has been observed to be negative in the three populations studied previously in maize (Coors, 1988; Edwards and Lamkey, 2002; Wardyn et al., 2007), general conclusions were difficult to draw. A theoretical observation, however, was possible. The component D_2^* (variance of homozygous dominance deviations; see materials and methods) affects response in

inbred offspring ($F_D > 0$) but does not affect response in noninbred offspring. Thus, D_2^* is a quantification of a form of heritable dominance but is only heritable with respect to selection among inbred individuals and response

observed in inbred individuals. Classical dominance variance, σ^2_D , does not contribute directly to selection response in any form; thus, the proposition of heritable dominance is unique to selection among inbred progeny and response in inbred offspring in the improved population.

The classical breeders equation, $R = Sh^2$, was readily obtained from Tables 3, 5, and 6 with $F_p = F_D = F_C = 0$ for selection among individuals with selection before pollination (parental control, p , of 2). A value for $2p\theta_0$ of 1 was obtained from Table 5 and a coefficient of $1 + F_p = 1$ from Table 3 for σ^2_A , resulting in a numerator of σ^2_A , and the genetic portion of the denominator of $\sigma^2_A + \sigma^2_D$ was obtained from Table 6, resulting in $R = S[\sigma^2_A / (\sigma^2_A + \sigma^2_D + \sigma^2_E)] = Sh^2$, the classical breeders equation. Generalizing this equation to inbred candidates and inbred offspring produced four different equations, summarized in Table 7.

The classical breeder's equation is related directly to the concept of narrow-sense heritability, which in turn is tied directly to the concept of breeding value. Narrow-sense heritability is defined formally as a ratio of additive genetic variance to phenotypic variance, but it can also be interpreted as the regression of breeding value on phenotypic value (Falconer and Mackay, 1996). Operationally, the numerator in selection response is the genotypic covariance between offspring value and parent value, which is the numerator of the regression of offspring on parent or the numerator of the regression of breeding value on phenotypic value (Falconer and Mackay, 1996; Lynch and Walsh, 1998), at least for noninbred individuals. However, with inbreeding in either candidates or offspring, the covariance between candidates and offspring is not equivalent to additive genetic variance, and hence, the regression of offspring on parent is not equivalent to regression of breeding value (by the classical definition) on phenotype. Thus, additional work may be needed to address the question of how breeding value should be defined for inbred candidates and offspring of selected candidates.

In addition to the theoretical gap in quantitative genetics with regard to defining a concept of breeding value for inbred individuals, an additional need exists to design selection programs to reduce inbreeding depression. Based on published negative estimates of the covariance parameter D_1 , selection for outbred performance is likely, at least in some maize populations, to increase inbreeding depression rates. Additional work is needed to establish the generality of this expectation (increased inbreeding

depression with outbred selection) and if it is a general problem, to use the theory outlined here to develop more efficient strategies to reduce inbreeding depression.

CONCLUSIONS

It has been shown that three general forms of selection—individual, half-sib, and self-progeny—are predicted to change the rate of inbreeding depression in randomly mated populations, regardless of the inbreeding level of candidates. It was further established that selection among non-inbred candidates in three maize populations is predicted to increase the magnitude of inbreeding depression based on published estimates of the covariance parameter D_1 . Finally, it was shown that additional work is needed in quantitative genetics to develop an appropriate definition of breeding value for inbred individuals and to develop improved selection methods to reduce inbreeding depression.

APPENDIX

Multivariate Normal Derivation of Genetic Gain

The exact effect of inbreeding on genetic gain when candidates and offspring may have different inbreeding levels was not inherently obvious on the basis of existing genetic gain equations. Hence, a genetic gain equation was rederived from the multivariate normal distribution to be certain that population means of both candidates and offspring were properly accounted for. The goal was to predict the genotypic value, G_O , of an offspring individual, R or D, based on observed phenotypes of candidate families (Fig. 1). A candidate family descended from the same parent, P_m , as the male parent of individual R was referred to as the male candidate. The male candidate could consist of a family of individuals or a single individual. Likewise, the candidate family descended from the female parent, P_f of individual R was referred to as the female candidate. The variance of the vector of phenotypes and offspring genotypic value was

$$V \begin{pmatrix} P_m \\ P_f \\ G_O \end{pmatrix} = \begin{pmatrix} \sigma_{P(m)}^2 & 0 & \sigma_{m,O} \\ 0 & \sigma_{P(f)}^2 & \sigma_{f,O} \\ \sigma_{m,O} & \sigma_{f,O} & \sigma_{G(O)}^2 \end{pmatrix} \quad [A1]$$

where P_m = estimated phenotype of male candidate, P_f = estimated phenotype of female candidate, G_O = genotypic value (unobserved) of offspring, $\sigma_{P(m)}^2$ = phenotypic variance of male candidate, $\sigma_{P(f)}^2$ = phenotypic variance of female candidate, $\sigma_{G(O)}^2$ = genotypic variance of offspring, $\sigma_{m,O}$ = covariance between male candidate phenotype and offspring genotypic value, and $\sigma_{f,O}$ = covariance between female candidate phenotype and offspring genotypic value.

Table 7. Numerators and denominators for selection among individuals.

F_p	Numerator			Denominator
	$F_D = 1$	$F_D = 0$	Diff	
0	$\sigma_A^2 + D_1$	σ_A^2	D_1	$\sigma_A^2 + \sigma_D^2 + \sigma_E^2$
1	$2\sigma_A^2 + 4D_1 + D_2^*$	$2\sigma_A^2 + 2D_1$	$2D_1 + D_2^*$	$2\sigma_A^2 + 4D_1 + D_2^*$

From the variance–covariance matrix of the vector of candidates and offspring, the conditional mean of G_O was (Searle, 1971, p. 47)

$$E[G_O | P_m, P_f] = \mu_O + \frac{\sigma_{m,O}}{\sigma_{P(m)}^2} (P_m - \mu_m) + \frac{\sigma_{f,O}}{\sigma_{P(f)}^2} (P_f - \mu_f) \quad [A2]$$

where μ_O = expected genotypic value of offspring (without selection); μ_m = expected phenotypic value of male candidates, that is, $E[P_m] = \mu_m$; and μ_f = expected phenotypic value of female candidates, that is, $E[P_f] = \mu_f$.

Equation [A2] is very general because male and female candidate families can have different means, different phenotypic variances, and different covariances with offspring. Correct application of Eq. [A2] depends on a very clear understanding of Eq. [A1]. First, phenotypes of male and female candidates, P_m and P_f and their variances, $\sigma_{P(m)}^2$ and $\sigma_{P(f)}^2$, must correspond to each other. For example, if P_m is a best linear unbiased predictor (BLUP) from a mixed-model analysis, $\sigma_{P(m)}^2$ should be the total variance among BLUP estimators, $\text{var}(\hat{u})$. Further, the variance–covariance matrix shows that phenotypes of male and female candidates were assumed to be independent, meaning that no genetic relationship was assumed between male and female candidates. Account of inbreeding level is also needed with respect to P_m and P_f as population means, μ_m and μ_f need to be the mean of a population with the same inbreeding level as the male and female candidates.

Equation [A2] was simplified by assuming that male and female candidates had identical pedigree structures so that the two terms were identical. It was also assumed that selection could be on either both parents of individual R, or only a single parent of individual R with one parent of R selected at random from the population. The number of parents selected, i.e., parental control, was quantified with the term p which had values of 1 or 2 for number of selected parents. Replacing the “m” and “f” subscripts with a “C” for candidate and adding p for the number of selected parents:

$$E[G_O | \bar{x}_C] = \mu_O + p \frac{\sigma_{C,O}}{\sigma_{P(C)}^2} (\bar{x}_C - \mu_C) \\ = \mu_O + pS \frac{\sigma_{C,O}}{\sigma_{P(C)}^2} = \mu_O + pi \frac{\sigma_{C,O}}{\sigma_P} \quad [A3]$$

where $\sigma_{C,O}$ = covariance between candidates and offspring, $\sigma_{P(C)}^2$ = phenotypic variance of candidates, \bar{x}_C = mean

phenotype of candidates, S = selection differential, and i = standardized selection differential.

Equation [A3] shows explicitly the relationship between the mean of offspring, μ_o , and the mean of candidates, μ_c , in predicted genetic gain. The predicted mean of offspring with selection is predicted as a deviation from the mean of offspring without selection, μ_o , and a deviation of candidates from the candidate population mean, $\bar{x}_c - \mu_c$. Equation [A3] also shows substitutions of the selection differential $S = \bar{x}_c - \mu_c$, and the standardized differential, $i = S/\sigma_p$. Equation [A3] could be expressed as a predicted change in genetic value, ΔG , as in classical genetic gain equations:

$$\Delta G = pS \frac{\sigma_{C,O}}{\sigma_{P(C)}} = pi \frac{\sigma_{C,O}}{\sigma_{P(C)}} \quad [A4]$$

The limitation with an equation expressed in terms of ΔG with candidates and offspring possibly at different inbreeding levels is that an equation for ΔG leaves the impact of inbreeding through changes in offspring and candidate population means less explicit in the final equation.

Recursion Formulas for Descent Measures

For individuals X and D, let ϕ_{DX} be a generic descent measure for any number of alleles in X and a single allele in D and let ϕ_{XD} be a generic descent measure for any number of alleles in X and two alleles in D. Consider a pedigree in which individual D is a descendant of A with g generations between D and A. Assuming that D is related to X only through its relationship to individual A, simplified expressions were obtained for the relationship between D and X as functions of the relationship between A and X.

If individual D was derived exclusively by g generations of self-pollination, expansion from generation g to generation $g - 1$ of a generic descent measure that was a function of a single allele in individual D, ϕ_{DX} , took the following form (Cockerham, 1971):

$$\phi_{XD} = \frac{1}{2}(\phi_{XD_{g-1}} + \phi_{XD_{g-1}}) = \phi_{XD_{g-1}}$$

By induction, the expansion was carried backward through selfing generations to the original ancestor, A:

$$\phi_{XD} = \phi_{XA} \quad [A5]$$

The generic descent measure in Eq. [A5] was applied to specific measures that were functions of a single allele in D, namely $\theta_{XD} = \theta_{XA}$ and $\gamma_{XD} = \gamma_{XA}$.

In individual D was the result of an outcross, i.e., one gamete was randomly sampled from the base population, the expansion from generation $g - 1$ to generation g was $\phi_{XD} = \frac{1}{2}(\phi_{XD_{g-1}} + \phi_{Xr_{g-1}}) = \frac{1}{2}\phi_{XD_{g-1}}$, where $\phi_{Xr_{g-1}}$ = descent measure for individual X and a gamete randomly sampled from the base population, $\phi_{Xr_{g-1}} = 0$.

If generation $g - 1$ also resulted from an outcross, expansion to generation $g - 2$ produced $\phi_{XD} = \frac{1}{2}\phi_{XD_{g-1}} = \frac{1}{4}\phi_{XD_{g-2}}$.

By induction, for g generations of outcrossing (with no loops and no other relationships in the pedigree): $\phi_{XD} = (\frac{1}{2})^g \phi_{XA}$.

By Eq. [A5], generations of selfing between individuals A and D had no effect on the expansion from D to A for a measure that is a function of a single allele in D. Hence, to generalize for pedigrees with a mixture of self-pollination and outcrossing, the number of outcross generations, h , was substituted for the total number of generations:

$$\phi_{XD} = (\frac{1}{2})^h \phi_{XA} \quad [A6]$$

For descent measures that were functions of two alleles in D, γ_{XD} , Δ_{X+D} , Δ_{X-D} , δ_{XD} , and F_D , if D was an outcross, any measure that was a function of two alleles in D is zero. For the case of self-pollination, expansion to generation $g - 1$ produced $\phi_{XD_g} = \frac{1}{2}(\phi_{XD_{g-1}} + \phi_{XD_{g-1}}) = \frac{1}{2}(\phi_{XD_{g-1}} + \phi_{XA})$. This expression arose from the fact that the two alleles in D_g have a 1/2 probability of being copies of two different alleles in D, and a 1/2 probability of being two copies of the same allele in the previous generation, in which case by Eq. [A5], $\phi_{XD_{g-1}}$ can be expanded immediately all the way back to individual A by substituting ϕ_{XA} (Cockerham, 1971, 1983). Multiplication by two and subtraction of ϕ_{XA} produced $2\phi_{XD} - \phi_{XA} = \phi_{XD_{g-1}} - \phi_{XA}$, which was rearranged to obtain $(\phi_{XD_g} - \phi_{XA}) / (\phi_{XD_{g-1}} - \phi_{XA}) = 1/2$.

The numerator and denominator differ only in generational subscripts in the terms ϕ_{XD_g} and $\phi_{XD_{g-1}}$ so that any value can be substituted for the subscripts g in the subscripts of ϕ_{XD_g} and $\phi_{XD_{g-1}}$. The value $g - 1$ was substituted for g to obtain $(\phi_{XD_{g-1}} - \phi_{XA}) / (\phi_{XD_{g-2}} - \phi_{XA}) = 1/2$, which was multiplied by the original expression to obtain

$$\left(\frac{\phi_{XD_g} - \phi_{XA}}{\phi_{XD_{g-1}} - \phi_{XA}} \right) \left(\frac{\phi_{XD_{g-1}} - \phi_{XA}}{\phi_{XD_{g-2}} - \phi_{XA}} \right) = (1/2)(1/2)$$

The term $\phi_{XD_{g-1}} - \phi_{XA}$ canceled from both numerator and denominator, resulting in $(\phi_{XD_g} - \phi_{XA}) / (\phi_{XD_{g-2}} - \phi_{XA}) = 1/4$. By induction, if individual D was derived by g generations of self-pollination, the general transition to expand from D to A was

$$\left(\frac{\phi_{XD_g} - \phi_{XA}}{\phi_{XD_{g-g}} - \phi_{XA}} \right) = \left(\frac{\phi_{XD} - \phi_{XA}}{\phi_{XA} - \phi_{XA}} \right) = \left(\frac{1}{2} \right)^g$$

where $D_g = D$ and $D_{g-g} = A$.

The generic transition was applied to all descent measures that were functions of two alleles in individual D, γ_{XD} , Δ_{X+D} , Δ_{X-D} , δ_{XD} , and F_D , by substituting each of the individual measures for ϕ_{XD} . In the final transition equation, the measure $\phi_{XD_{g-g}} = \phi_{XA}$ represents a descent measure that is carried through every generation of expansion, so that the same descent measure was substituted for ϕ_{XA} as for ϕ_{XD} in the generic transition equation. For example,

if obtaining a transition for expansion of γ_{XD} by substituting γ_{XD} for ϕ_{XD} , γ_{XA} is substituted for ϕ_{XA} . The term ϕ_{XA} in the generic transition equation arose for the case when the two alleles in generation g were identical copies of the same allele in generation $g - 1$. Hence, for a particular transition equation, the descent measure to substitute for ϕ_{XA} was identified from the single generation expansion from generation g to generation $g - 1$ using expressions and methods from Cockerham (1971). Specific substitutions for all three generic terms in the transition equation are summarized in Table A1.

The general transition was applied to the inbreeding coefficient, F_{D} , and then to remaining measures to obtain further simplification:

$$\left(\frac{\phi_{\text{XD}} - \phi_{\text{XA}}}{\phi_{\text{XA}} - \phi_{\text{AA}}} \right) = \left(\frac{1}{2} \right)^g = \left(\frac{F_{\text{D}} - 1}{F_{\text{A}} - 1} \right) = \left(\frac{1 - F_{\text{D}}}{1 - F_{\text{A}}} \right)$$

which after algebraic rearrangement resulted in

$$\phi_{\text{XD}} = \frac{\phi_{\text{XA}} (F_{\text{D}} - F_{\text{A}}) + \phi_{\text{AA}} (1 - F_{\text{D}})}{1 - F_{\text{A}}} \quad [\text{A7}]$$

Variance of Family Means

The genotypic variance of a family mean was defined as the variance of the average genotypic value of all family members. Given a vector of observations, \mathbf{x} , with the i th observation having a variance $\sigma_{x_i}^2$ and covariance between elements i and j of $\sigma_{x_i x_j}$, the variance of the average of elements in \mathbf{x} is

$$\text{Var} \left(\frac{\sum \mathbf{x}}{n} \right) = \frac{1}{n} \sigma_{x_i}^2 + \frac{n-1}{n} \sigma_{x_i x_j}$$

The covariance between the average values of vectors \mathbf{x} and \mathbf{y} , with the covariance between any element within vectors being $\sigma_{x_i y_j}$ is

$$\text{Cov} \left(\frac{\sum \mathbf{x}}{n}, \frac{\sum \mathbf{y}}{n} \right) = \frac{1}{n^2} (n^2 \sigma_{x_i y_j}) = \sigma_{x_i y_j}$$

The variance and covariance formulas for averages were applied recursively to obtain the variance of the average genotypic value of a candidate family for predicted selection response. The genotypic covariance between candidate individuals in generation $t + i$ with last common ancestor in generation t was denoted $C_{t,t+i}$. If all individuals within a candidate family were direct descendants of a single individual (either half-sibs or full-sibs derived by self-pollination), the variance of the mean genotypic value of the family was

$$\sigma_{\text{G(C)}}^2 = \frac{1}{n_1} C_{t+1,t+1} + \frac{n_1-1}{n_1} C_{t,t+1} \quad [\text{A8}]$$

Table A1. Summary of expansions of generic descent measure ϕ_{XD} from individual D to individual A for Eq. [A7].

ϕ_{XD}	Expand D [†]	Expansion formula [‡]	ϕ_{XA}	ϕ_{AA}
γ_{XD}	$\gamma_{\text{X(D}_g\text{-D}_{g-1})}$	$\frac{1}{2} (\gamma_{\text{XD}_{g-1}} + \theta_{\text{XD}_{g-1}})$	γ_{XA}	θ_{XA}
δ_{XD}	$\delta_{\text{X(D}_g\text{-D}_{g-1})}$	$\frac{1}{2} (\delta_{\text{XD}_{g-1}} + \gamma_{\text{XD}_{g-1}})$	δ_{XA}	γ_{XA}
Δ_{XD}	$\Delta_{\text{X(D}_g\text{-D}_{g-1})}$	$\frac{1}{2} (\Delta_{\text{XD}_{g-1}} + F_{\text{X}})$	Δ_{XA}	1
Δ_{XD}	$\Delta_{\text{X(D}_g\text{-D}_{g-1})}$	$\frac{1}{2} (\Delta_{\text{XD}_{g-1}} + \gamma_{\text{XD}_{g-1}})$	Δ_{XA}	γ_{XA}
F_{D}	$F_{\text{(D}_g\text{-D}_{g-1})}$	$\frac{1}{2} (F_{\text{D}_{g-1}} + 1)$	F_{A}	1

[†]Individual D was expanded from generation g to generation $g - 1$.

[‡]Specific expressions for descent measures when two random alleles are sampled from a single individual were obtained from Cockerham (1971).

The genotypic variances and covariances in the expression for the variance of mean genotypic values were expressed with respect to the base population; for example, $C_{t+1,t+1}$ was not assumed to be the variance within candidate families but was total genotypic variance among individuals in generation $t + 1$. If two generations of reproduction (by either outcrossing to produce half-sibs, selfing, or a combination of outcrossing and selfing) were required, the two formulas were applied recursively to obtain

$$\sigma_{\text{G(C)}}^2 = \frac{1}{n_1} \left(\frac{1}{n_2} C_{t+2,t+2} + \frac{n_2-1}{n_2} C_{t+1,t+2} \right) + \frac{n_1-1}{n_1} C_{t,t+2} \quad [\text{A9}]$$

where n_1 = number of offspring sampled in $t + 1$, and n_2 = number of offspring sampled generation $t + 2$ from each individual in generation $t + 1$.

A third recursion was applied for the case in which three generations were required to obtain adequate quantities of seed

$$\sigma_{\text{G(C)}}^2 = \frac{1}{n_1} \left[\frac{1}{n_2} \left(\frac{1}{n_3} C_{t+3,t+3} + \frac{n_3-1}{n_3} C_{t+2,t+3} \right) + \frac{n_2-1}{n_2} C_{t+1,t+3} \right] + \frac{n_1-1}{n_1} C_{t,t+3} \quad [\text{A10}]$$

where n_1 = number of individuals sampled in generation t , n_2 = number of individuals sampled in generation $t + 1$, and n_3 = number of individuals sampled in generation $t + 2$.

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